

October 2007

Exceptionally Preserved Jellyfishes from the Middle Cambrian

Paulyn Cartwright
University of Kansas

Susan L. Halgedahl
University of Utah

Jonathan R. Hendricks
University of Kansas, hendricks@priweb.org

Richard D. Jarrard
University of Utah

Antonio C. Marques
Universidade de São Paulo

See next page for additional authors

Follow this and additional works at: https://scholarworks.sjsu.edu/geol_pub

 Part of the [Geology Commons](#)

Recommended Citation

Paulyn Cartwright, Susan L. Halgedahl, Jonathan R. Hendricks, Richard D. Jarrard, Antonio C. Marques, Allen G. Collins, and Bruce S. Lieberman. "Exceptionally Preserved Jellyfishes from the Middle Cambrian" *PLoS ONE* (2007). doi:10.1371/journal.pone.0001121

This Article is brought to you for free and open access by the Geology at SJSU ScholarWorks. It has been accepted for inclusion in Faculty Publications by an authorized administrator of SJSU ScholarWorks. For more information, please contact scholarworks@sjsu.edu.

Authors

Paulyn Cartwright, Susan L. Halgedahl, Jonathan R. Hendricks, Richard D. Jarrard, Antonio C. Marques, Allen G. Collins, and Bruce S. Lieberman

Exceptionally Preserved Jellyfishes from the Middle Cambrian

Paulyn Cartwright¹, Susan L. Halgedahl², Jonathan R. Hendricks³, Richard D. Jarrard², Antonio C. Marques⁴, Allen G. Collins⁵, Bruce S. Lieberman^{3*}

1 Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas, United States of America, **2** Department of Geology and Geophysics, University of Utah, Salt Lake City, Utah, United States of America, **3** Department of Geology, and Division of Invertebrate Paleontology, Natural History Museum, University of Kansas, Lawrence, Kansas, United States of America, **4** Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, São Paulo, Brazil, **5** National Systematics Laboratory of NOAA Fisheries Service, National Museum of Natural History, Smithsonian Institution, Washington, D. C., United States of America

Cnidarians represent an early diverging animal group and thus insight into their origin and diversification is key to understanding metazoan evolution. Further, cnidarian jellyfish comprise an important component of modern marine planktonic ecosystems. Here we report on exceptionally preserved cnidarian jellyfish fossils from the Middle Cambrian (~505 million years old) Marjum Formation of Utah. These are the first described Cambrian jellyfish fossils to display exquisite preservation of soft part anatomy including detailed features of structures interpreted as trailing tentacles and subumbrellar and exumbrellar surfaces. If the interpretation of these preserved characters is correct, their presence is diagnostic of modern jellyfish taxa. These new discoveries may provide insight into the scope of cnidarian diversity shortly after the Cambrian radiation, and would reinforce the notion that important taxonomic components of the modern planktonic realm were in place by the Cambrian period.

Citation: Cartwright P, Halgedahl SL, Hendricks JR, Jarrard RD, Marques AC, et al (2007) Exceptionally Preserved Jellyfishes from the Middle Cambrian. PLoS ONE 2(10): e1121. doi:10.1371/journal.pone.0001121

INTRODUCTION

The phylum Cnidaria is one of the earliest branching animal groups to display organized tissues and a nervous system [1]. Cnidaria has a primary divergence between two large clades, Anthozoa, corals and sea anemones, and Medusozoa, including scyphozoans (true jellyfish), cubozoans (box jellies), hydrozoans (hydroids, *Hydra*, and hydromedusae) and staurozoans (stalked medusae) [2]. Typically, medusozoan cnidarians have a pelagic, predatory jellyfish stage in their life cycle; staurozoans are the exceptions. The predatory life-style is accompanied by sense organs and sophisticated behavior, although little is known about the evolution of these complex traits. Because of their early origin within Metazoa, genomic and developmental studies of cnidarians are yielding important insights into the unfolding of animal diversity, e.g., [3–5]. The early divergence of cnidarians in animal phylogeny leaves little doubt of their presence in the Cambrian; however, there have been no previous reports of fossils possessing preserved characters diagnostic of particular medusozoan clades. The absence of preservation detail in medusozoan fossils has thus far hampered our knowledge of the extent of cnidarian diversity and complexity that existed during this key time in animal evolution.

Many fossils of soft-bodied medusoid-like animals have been reported from the late Neoproterozoic and Cambrian, but the lack of diagnostic characters obscures their phylogenetic provenance [6]. Fossil chondrophores (family Porpitidae) are the only possible evidence for crown group hydrozoans during the Late Proterozoic and Cambrian [6–11] but see [12]. Porpitids, however, are not true medusae, and instead are pelagic colonies whose individual members are organized around a large central mouth. Many previously described non-porpitid medusoid-like forms from the Ediacaran and Cambrian are preserved as circular impressions in siliciclastic or calcareous sediments thought to have been deposited in shallow marine conditions [13,14]. Typically, these fossils are preserved in low relief and often display concentric internal rings that are sometimes overlapped by radiating lines. Most of these

medusoid-like fossils lack distinctive evidence of soft-part anatomy, such as tentacles, mouths, or sense organs, and some have been reinterpreted as Ediacaran-like organisms, trace fossils, or abiotic pseudofossils [9,15–17]. Medusoid fossils have been reported from the Mt. Simon-Wonewoc Sandstone (Upper Cambrian of Wisconsin, USA) and these appear to represent true medusozoans; however, because of their incomplete state of preservation, related to aspects of taphonomy [18], diagnostic characters of modern medusozoan classes were not preserved [19]. To date, the only Paleozoic fossils that definitively possess diagnostic medusozoan characters are from the Mazon Creek biota (Pennsylvanian of Illinois, USA) [20] and the Wea Shale (Pennsylvanian of Iowa, USA) [21].

Here we report exceptionally well-preserved medusozoan fossils from the Middle Cambrian Marjum Formation of Utah, USA. In contrast to the taphonomic expression of other Cambrian and Neoproterozoic medusoid fossils, which are impressions in coarse sediments, these new medusoid fossils exhibit Burgess Shale-type preservation [22] and are preserved as organic compressions on very fine-grained marine sediments. This allows the potential recovery of more detailed anatomical information, although it also

Academic Editor: Stuart Humphries, University of Sheffield, United Kingdom

Received: September 16, 2007; **Accepted:** October 15, 2007; **Published:** October 31, 2007

Copyright: © 2007 Cartwright et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: This work was supported by grants from NSF ATOL EF-0531779 (to PC and AGC), NSF EAR-0518976 (to BSL) and FAPESP and CNPq (Brazil, to ACM).

Competing Interests: The authors have declared that no competing interests exist.

* To whom correspondence should be addressed. E-mail: blieber@ku.edu

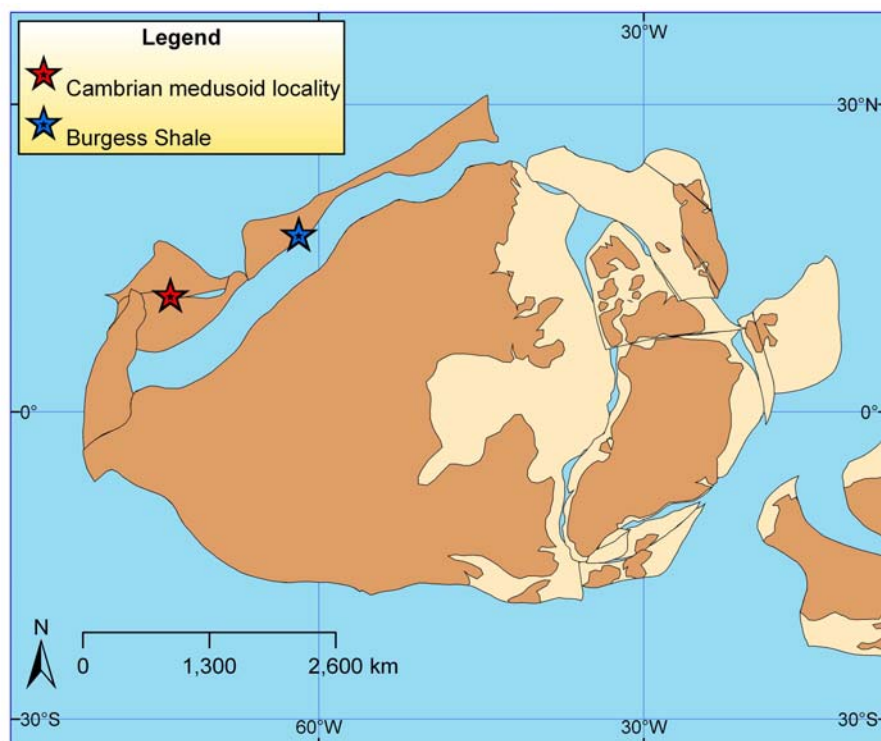


Figure 1. Paleogeographic reconstruction for the Middle Cambrian emphasizing the position of North America. Approximate positions of locality in Utah yielding fossil jellyfishes and the site of the famous Burgess Shale are marked as indicated. Map derived using [41]. doi:10.1371/journal.pone.0001121.g001

entails that different specimens will show different features due to several preservational factors including how they are orientated to sediment bedding planes [23]. While the precise taphonomic processes responsible for preserving the remains of non-skeletonized soft-bodied animals, such as these medusozoans in the Marjum Formation, have not been studied in great detail, they have been considered for other soft-bodied remains derived from the slightly older Middle Cambrian Wheeler Formation of Utah by [24]. [24] have hypothesized that the mode of preservation in the two formations is likely similar, with factors associated with anoxic bottom waters that limit sediment permeability, bioturbation, and microbial-related decay facilitating the preservation of the exquisite detail of these soft-bodied remains. In this respect, soft-bodied preservation in the Marjum Formation is similar to what is known from the famous Burgess Shale [25]. Still, even with the level of detail preserved, we hesitate to definitively assign any of these fossils to a specific taxon because taphonomic factors can conspire to make particular features of specimens difficult to interpret and even modern jellyfish possess few diagnostic features. We do, however, discuss distinctive features exhibited by these specimens that indicate they share affinities with certain modern cnidarian clades.

MATERIALS AND METHODS

All fossil specimens were collected by co-authors SLH and RDJ and are from the Marjum Formation, Middle Cambrian, Utah, the Sponge Gully Locality, 39°16.143'N, 113°18.597'W. This locality, which has been described in detail previously [26–28] (Figs. 1, 2), yields a diverse biota of soft-bodied taxa and trilobites in inter-bedded mudstones and thin-bedded, fine-grained limestones. These rocks are inferred to represent deposition in a warm water environment on a gently sloping ramp below storm wave

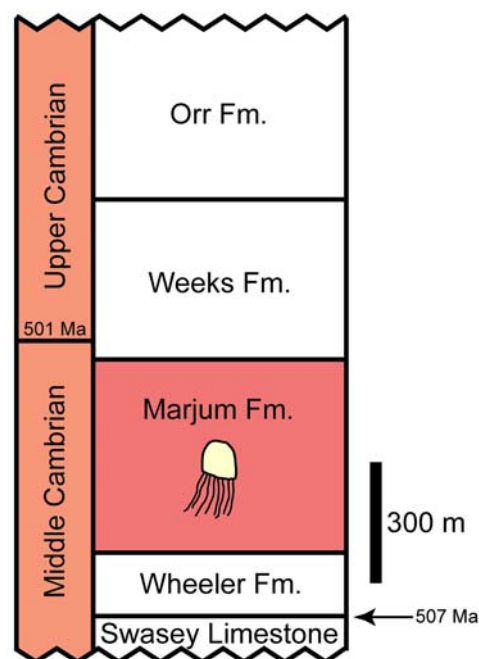


Figure 2. Stratigraphic column for Utah emphasizing Cambrian strata in the region where the new jellyfishes were collected. The new fossils come from an interval approximately 41–48 meters above the base of the Marjum Formation [26,27]; approximate ages of some stratigraphic horizons are shown. doi:10.1371/journal.pone.0001121.g002

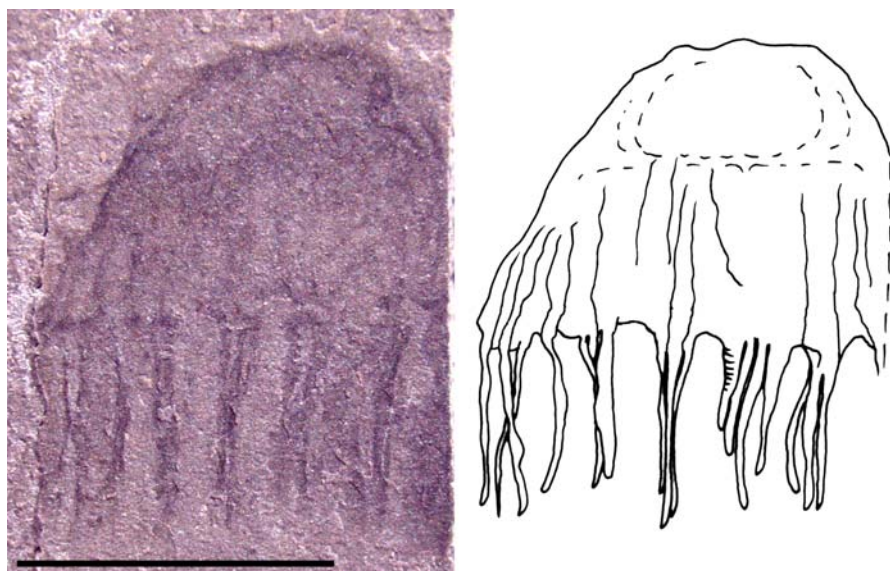


Figure 3. Photograph and interpretive drawing of Middle Cambrian cnidarian jellyfish in lateral view possibly referable to the family Narcomedusae, class Hydrozoa. Specimen UU07021.03, scale bar equals 5 mm.
doi:10.1371/journal.pone.0001121.g003

base [27,28]. Specimens occur in thin (~1 cm) fine-grained, dark grey mudstone beds that oscillate with thinner, more coarse-grained layers that weather to a reddish color.

RESULTS

Five specimens, UU [University of Utah] 07021.03 (Fig. 3), UU07021.04 (Fig. 4), UU07021.06, UU07021.07 and UU07021.08, appear to represent cnidarian medusozoans and have prominent umbrellas and trailing tentacles. In these specimens, the umbrella widths are greater than the umbrella heights, with a maximum width of 8.8 mm and a maximum height of

6.3 mm. Further, there are at least twelve solid tentacles, 3.7 mm in maximum length. The tentacles appear to arise on the exumbrella at some distance from the umbrellar margin. Due to the limited number of preserved characters it is difficult to determine how these specimens should be classified within Medusozoa. However, members of the hydrozoan family Narcomedusae do possess similar relative umbrella dimensions and have tentacle insertions above the umbrellar margin, suggesting that UU07021.03, UU07021.04, UU07021.06, UU07021.07 and UU07021.08 may possibly be narcomedusae.

Two other specimens, UU07021.09 and UU07021.10 (Figs. 5–8), also appear to represent cnidarian medusozoans; however, these specimens display other characteristics distinct from the



Figure 4. Photograph of Middle Cambrian cnidarian jellyfish in oblique subumbrellar view possibly referable to the family Narcomedusae, class Hydrozoa. Specimen UU07021.04, scale bar equals 5 mm.
doi:10.1371/journal.pone.0001121.g004

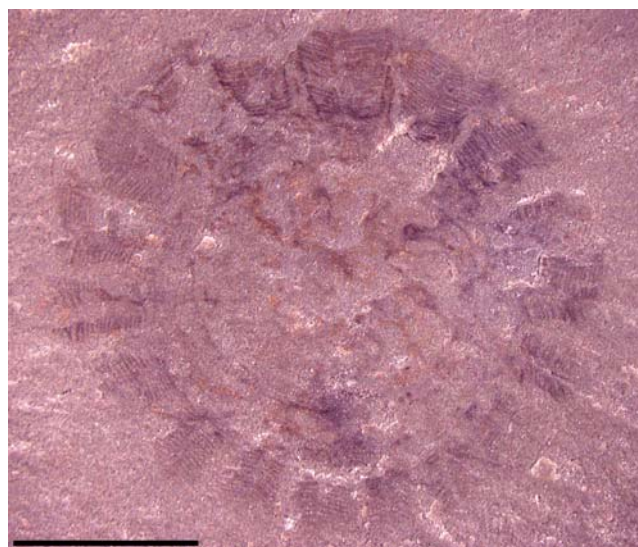


Figure 5. Photograph of Middle Cambrian cnidarian jellyfish in subumbrellar view possibly referable to the order Semaestomeae, class Scyphozoa. Specimen UU07021.09, scale bar equals 5 mm.
doi:10.1371/journal.pone.0001121.g005

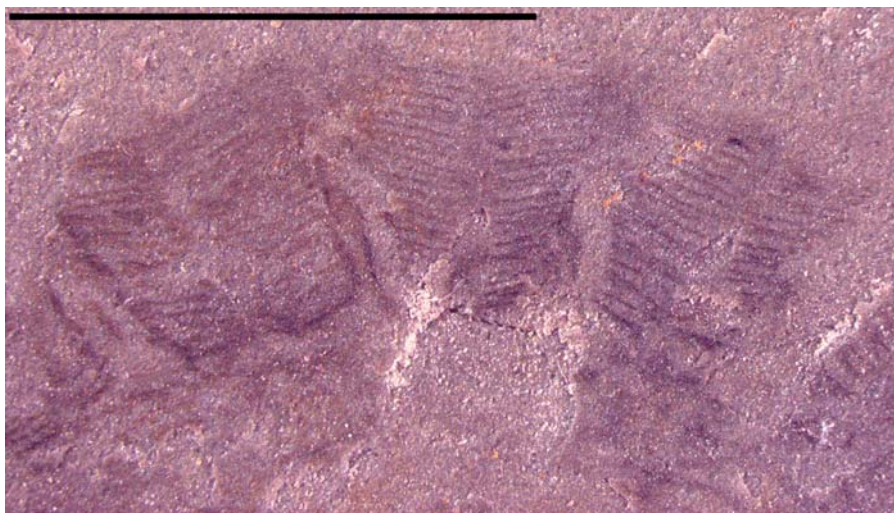


Figure 6. Close-up photograph showing structures interpreted as radially arranged coronal muscles. Specimen UU07021.09.
doi:10.1371/journal.pone.0001121.g006

aforementioned material and instead share similarities with cnidarian jellyfish belonging to the class Scyphozoa. The specimen in Figure 5 is interpreted as a subumbrellar view of a jellyfish showing 18 pairs of radially arranged muscles; muscles are shown in a close-up view in Figure 6. These muscles are similar to the swimming musculature in an extant order of scyphozoans, the Semaestomeae, which is arranged as a continuous coronal muscle interrupted by radial folds of the gastric cavity [29]. The outer margin of the umbrella in UU07021.09 is not preserved. UU07021.10 also appears to be a similar jellyfish but oriented laterally (Fig. 7). This specimen displays three horseshoe shaped structures (Fig. 8) that may be folded gonads, similar to those found in some extant semaestomes [29]. The presence and



Figure 7. Photograph of Middle Cambrian cnidarian jellyfish in lateral view possibly referable to the order Semaestomeae, class Scyphozoa. Specimen UU07021.10, scale bar equals 5 mm.
doi:10.1371/journal.pone.0001121.g007

arrangement of the swimming musculature and the possible presence of folded gonads are consistent with an assignment of these jellyfish to the scyphozoan order Semaestomeae, but given the uncertainties in preservation this assignment is made tentatively.

Another cnidarian specimen, UU07021.05 (Fig. 9), shares similarities with a different order of scyphozoan jellyfish. For instance, it appears to have a dome-shaped umbrella, with a maximum height of 7.4 mm (obliquely oriented) and a maximum width of 7.1 mm, although the shape of the umbrella may be distorted because of the preservation of the specimen. There also appears to be a deep groove encircling the basal third of the exumbrellar surface which, due to its position on the umbrella relative to the tentacles, bears a resemblance to a coronal groove, a feature common to the scyphozoan order Coronatae. Distal to the umbrellar margin there appears to be at least six pointed lappets (approximately 1.1 mm in length from coronal groove to distal part of lappet) with the bases of the tentacles arising between successive lappets. The apparent shape of the bell, presence of probable pointed lappets, relative position of the tentacles to these lappets, and the presence of a coronal groove are all characteristics of the scyphozoan order Coronatae, but the lack of additional specimens makes it difficult to assign this specimen conclusively to that taxon. A Paleozoic coronate, *Octomedusa pieckorum*, has been described previously from the Mazon Creek biota (Pennsylvanian of Illinois, USA) [20].

Finally, two other specimens, UU07021.01 and UU07021.02, appear distinct from the aforementioned material and have a box-shaped umbrella, with a maximum height of 6.3 mm, a maximum width of 7.2 mm, and a slightly concave apical region (Figs. 10, 11). There are thickenings at the proximal ends of the tentacles that are interpreted as pedalia. These pedalia are 2.8 mm in maximum height and 2.9 mm in maximum diameter. Each pedaliu has one tentacle associated with it. The specimen in Figure 10 appears to display a central cluster of three pedalia and tentacles with two other clusters on either side. Tentacles have a maximum length of 5.2 mm and possess transverse lines, resembling chains of discs, that are interpreted as nematocyst batteries. Many cnidarians, including cubozoans, have nematocysts arranged in transverse rows or lines in the outer tissue of the tentacles and these form circumferential bands of nematocyst

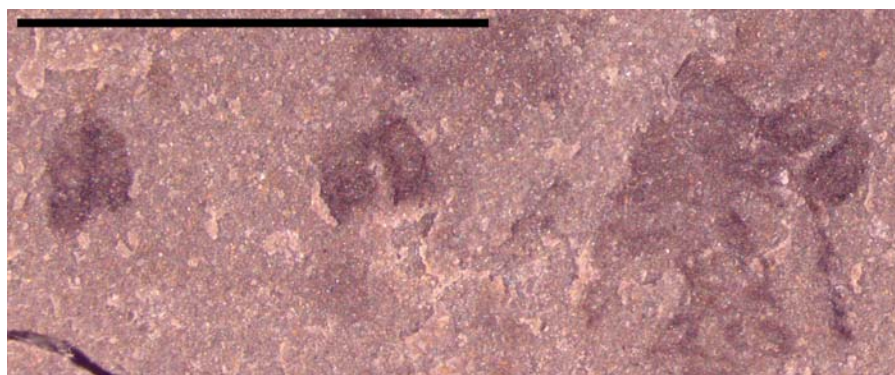


Figure 8. Close-up photograph showing structures interpreted as folded gonads. Specimen UU07021.10, scale bar equals 2.5 mm; these structures are visible in the upper middle part of Figure 10.
doi:10.1371/journal.pone.0001121.g008

batteries [30]. These transverse nematocyst batteries are particularly evident in contracted tentacles [31]. It is true that fossil ctenophores also feature transverse lines that represent ctenes of comb rows [32]. However, the material illustrated here differs from ctenophore comb rows because there is a clear outer margin outlining the tentacles: this is absent in comb rows. In addition, the tentacles in the specimens reported here hang below the umbrellar margin (Figs. 10, 11). This is typical of cnidarian medusae and differs markedly from ctenophores, whose comb rows run along the entire oral/aboral axis of the body, e.g., see [33].

The square shape of the umbrella, the presence of pedalia, tentacles, and nematocyst batteries, as well as the arrangement of the tentacles around the umbrellar margin in specimens UU07021.01 and UU07021.02, are all characters of the class Cubozoa. We acknowledge that among the aforementioned traits umbrellar shape is most likely to be governed by taphonomic

preservation; still, even setting this trait aside, in total these specimens show strongest affinities to this class of cnidarian jellyfish. The more than 30 extant species of Cubozoa [34] belong to two families: Carybdeidae, characterized by simple pedalia, each with one tentacle; and Chiropsidae, characterized by branched pedalia, each branch with its own tentacle. The only other reported Paleozoic cubozoan, *Anthracomedusa turnbulli* Johnson & Richardson, 1968, is from the Pennsylvanian Mazon Creek biota (Illinois, USA), and has been assigned to the Chiropsidae [20]. The new fossil material shows more traits in common with the Carybdeidae because the pedalia are simple and unbranched. However, given that taphonomic factors including incomplete preservation and orientation to bedding could influence the geometry of these structures, it is not possible to demonstrate conclusively that this material is referable to the Carybdeidae or even the Cubozoa.



Figure 9. Photograph and interpretive drawing of Middle Cambrian cnidarian jellyfish in oblique lateral view possibly referable to the order Coronatae, class Scyphozoa. Specimen UU07021.05, scale bar equals 5 mm. Structure marked Cg in drawing interpreted as a coronal groove; structures marked L interpreted as lappets; structures marked T interpreted as tentacles.
doi:10.1371/journal.pone.0001121.g009

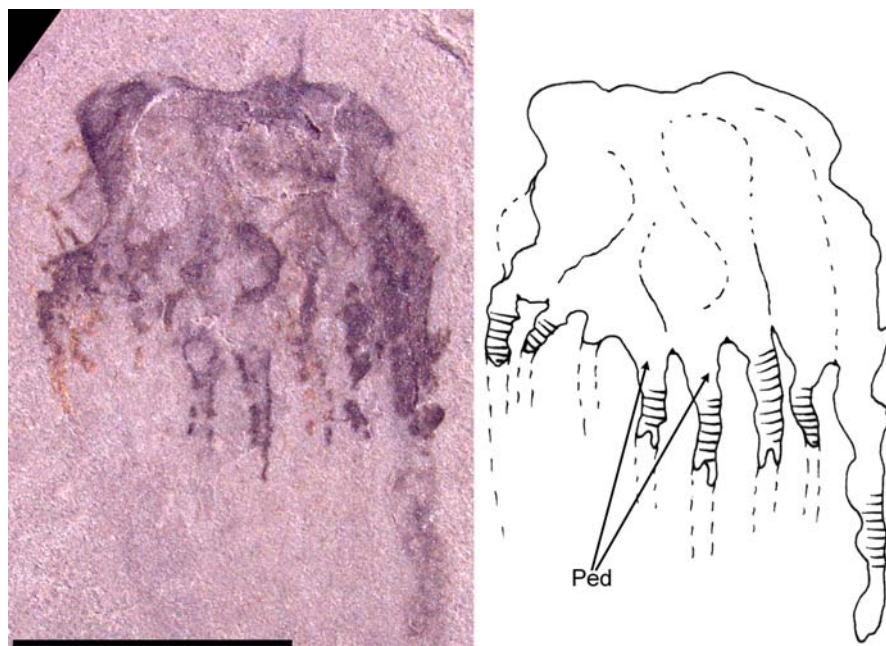


Figure 10. Photograph and interpretive drawing of Middle Cambrian cnidarian jellyfish in lateral view possibly referable to the class Cubozoa. Specimen UU07021.01, scale bar equals 5 mm. Structures marked *Ped* in drawing are interpreted as pedalia.
doi:10.1371/journal.pone.0001121.g010

DISCUSSION

These Middle Cambrian fossils are the oldest reported putative cnidarian jellyfish to display characteristics diagnostic of particular medusozoan taxa. If the preserved characters described herein are indeed consistent attributes of the fossil organisms, and not artifacts of taphonomy, then these Middle Cambrian fossils would be the oldest definitive crown-group jellyfish. Given the available

character information, they also may comprise representatives of three separate classes of modern medusozoans: Cubozoa; Hydrozoa; and Scyphozoa. This suggests that an important aspect of modern marine pelagic ecosystems was in place shortly after the Cambrian radiation.

Extant medusozoans possess several complex characters. For example, the living cubozoan *Tripedalia cystophora* has sophisticated reproductive behavior that includes mate recognition and courtship, involving the indirect transfer of sperm through spermatophores [35]. Cubozoans also have complex eyes [36] and nervous systems [37]. The existence of our newly described fossil material may suggest that these complex traits could have evolved within the Cnidaria by the Middle Cambrian.

Finally, fossil anthozoans have recently been reported from the early Cambrian [38], while conulariids, which have a phylogenetic origin within the Medusozoa [39], are known from the Late Cambrian [40]. Taken in combination with the fossils discussed here, which may represent hydrozoans, scyphozoans, and cubozoans, it suggests that the modern cnidarian classes had evolved by the Cambrian. Further, some of these fossils share commonalities with modern cnidarian orders and families; this may indicate that a significant amount of diversification within the Cnidaria had also occurred by the Cambrian.

ACKNOWLEDGMENTS

We thank D.E.G. Briggs, A. Migotto, A. Morandini, and R.A. Robison for discussions and A. Nawrocki, L. Trueb, PLoS ONE editor S. Humphries, and anonymous reviewers for comments on earlier versions of this manuscript. M. Garfield and K. Anderson assisted with illustrations.

Author Contributions

Conceived and designed the experiments: PC BL JH SH RJ AM AC. Analyzed the data: PC BL JH SH RJ AM AC. Wrote the paper: PC BL JH SH RJ AM AC.

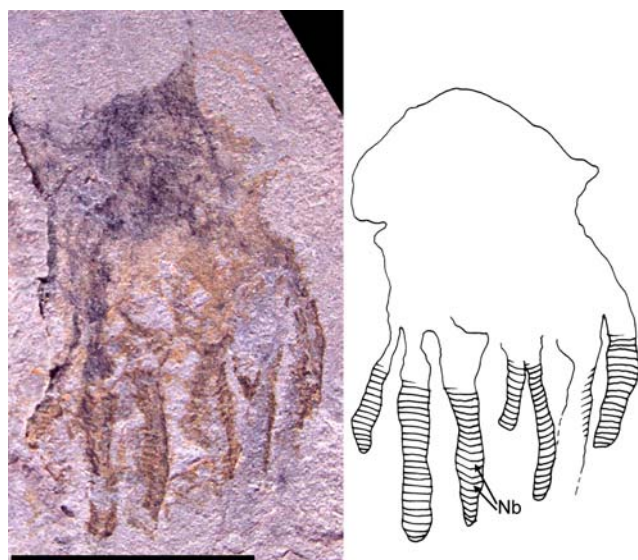


Figure 11. Photograph and interpretive drawing of Middle Cambrian cnidarian jellyfish in lateral view possibly referable to the class Cubozoa. Specimen UU07021.02, scale bar equals 5 mm. Structures marked *Nb* in drawing are interpreted as nematocyst batteries.
doi:10.1371/journal.pone.0001121.g011

REFERENCES

- Nielsen C, Scharff N, Eibye-Jacobsen D (1996) Cladistic analyses of the animal kingdom. *Biol J Linn Soc* 57: 385–410.
- Marques AC, Collins AG (2004) Cladistic analysis of Medusozoa and cnidarian evolution. *Invert Biol* 123: 23–42.
- Finnerty JR, Pang K, Burton P, Paulson D, Martindale MQ (2004) Origins of bilateral symmetry: Hox and Dpp expression in a sea anemone. *Science* 304: 1335–1337.
- Kusserow A, Pang K, Sturm C, Hrouda M, Lentfer J, et al. (2005) Unexpected complexity of the Wnt gene family in a sea anemone. *Nature* 433: 156–160.
- Putnam NH, Srivastava M, Hellsten U, Dirks B, Chapman J, et al. (2007) Sea anemone genome reveals ancestral eumetazoan gene repertoire and genomic organization. *Science* 317: 86–94.
- Conway Morris S (1993) Ediacaran-like fossils from the Cambrian Burgess Shale type faunas of North America. *Palaeontology* 36: 593–565.
- Glaessner MF, Wade M (1966) The Late Precambrian fossils from Ediacara, South Australia. *Paleontology* 9: 599–628.
- Narbonne GM (2005) The Ediacara biota; Neoproterozoic origin of animals and their ecosystems. *Ann Rev Earth Planet Sci* 33: 421–442.
- Narbonne GM, Myrow P, Landing E, Anderson MM (1991) A chondrophorine (medusoid hydrozoan) from the basal Cambrian (Placentian) of Newfoundland. *J Paleontol* 65: 186–191.
- Stanley GD Jr (1986) Chondrophorine hydrozoans as problematic fossils. In: Hoffman A, Nitecki MH, eds. *Problematic fossil taxa*. Oxford [Oxfordshire]: Oxford University Press. pp 68–86.
- Wade M (1971) Bilateral Precambrian chondrophores from the Ediacara fauna, South Australia. *Proc R Soc Victoria* 84: 183–188.
- Waggoner BM, Collins AG (1995) A new chondrophorine (Cnidaria, Hydrozoa) from the Cadiz Formation (Middle Cambrian) of California. *Palaeontol Zeit* 69: 7–17.
- Walcott CD (1911) Cambrian geology and paleontology II, No. 3 - Middle Cambrian holothurians and medusae. *Smith Misc Coll* 57: 41–69.
- Willoughby RH, Robison RA (1979) Medusoids from the Middle Cambrian of Utah. *J Paleontol* 53: 494–500.
- Fedonkin MA, Runnegar BN (1992) Proterozoic metazoan trace fossils. In: Schopf JW, Klein C, eds. *The Proterozoic Biosphere: A Multidisciplinary Study*. Cambridge: Cambridge University Press. pp 389–395.
- Gehling JG, Narbonne GM, Anderson MM (2000) The first named Ediacaran body fossil; *Aspidella terranovica*. *Palaeontology* 43: 427–456.
- Plummer PS (1980) Circular structures in a late Precambrian sandstone; fossil medusoids or evidence of fluidization? *Trans Royal Soc S Aust* 104: 13–15.
- Norris RD (1989) Cnidarian taphonomy and the affinities of Ediacaran biota. *Lethaia* 22: 381–393.
- Hagadorn JW, Dott RHJ, Damrow D (2002) Stranded on a Late Cambrian shoreline: Medusae from central Wisconsin. *Geology* 30: 147–150.
- Johnson RG, Richardson ES Jr (1968) Pennsylvanian invertebrates of the Mazon Creek area, Illinois: The Essex fauna and medusae. *Fieldiana: Geology (New Series)* 12: 109–115.
- Ossian CR (1973) New Pennsylvanian scyphomedusan from western Iowa. *Journal of Paleontology* 47: 990–995.
- Butterfield NJ (1997) Plankton ecology and the Proterozoic-Phanerozoic transition. *Paleobiology* 23: 247–262.
- Allison PA, Briggs DEG (1993) Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. *Geology* 21: 527–530.
- Gaines RR, Kennedy MJ, Droser ML (2005) A new hypothesis for organic preservation of Burgess Shale taxa in the middle Cambrian Wheeler Formation, House Range, Utah. *Palaeogeog, Palaeoclimat, Palaeoecol* 220: 193–205.
- Allison PA, Brett CE (1995) *In situ* benthos and paleo-oxygenation in the Middle Cambrian Burgess Shale, British Columbia, Canada. *Geology* 23: 1079–1082.
- Briggs DEG, Robison RA (1984) Exceptionally preserved nontrilobite arthropods and Anomalocaris from the Middle Cambrian of Utah. *Univ Kansas Paleontol Contribs*, Paper 111: 1–24.
- Conway Morris S, Robison RA (1986) Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. *Univ Kansas Paleontol Contribs*, Paper 117: 1–22.
- Robison RA (1991) Middle Cambrian biotic diversity: examples from four Utah lagerstätten. In: Simonetta AM, Conway-Morris S, eds. *The Early Evolution of Metazoa and the Significance of Problematic Taxa*. Cambridge: Cambridge University Press. pp 77–98.
- Russell FS (1970) *The Medusae of the British Isles. Vol. II - Pelagic Scyphozoa, with a supplement to Vol. I*. Cambridge: Cambridge University Press.
- Yanagihara AA, Kuroiwa JMY, Oliver LM, Chung JJ, Kunkel DD (2002) Ultrastructure of a novel urytelet nematocyst of *Carybdea alata* Reynaud (Cubozoa, Cnidaria). *Cell Tissue Res* 308: 307–318.
- Campbell RD (1987) Organization of the nematocyst battery in the tentacle of *Hydra*: Arrangement of the complex anchoring junctions between nematocytes, epithelial cells, and basement membrane. *Cell Tissue Res* 249: 647–655.
- Conway Morris S, Collins DH (1996) Middle Cambrian ctenophores from the Stephen Formation, British Columbia, Canada. *Phil Trans Biol Sci* 351: 279–308.
- Hou X-G, Aldridge RJ, Bergström J, Siveter DJ, Siveter DJ, Feng X-H (2004) *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life*. London: Blackwell.
- Gershwin L, Alderslade P (2005) A new genus and species of box jellyfish (Cubozoa: Carybdeidae) from tropical Australian waters. *The Beagle, Recs Mus Art Gall N Terr* 21: 27–36.
- Lewis C, Long TAF (2005) Courtship and reproduction in *Carybdea sivickisi* (Cnidaria: Cubozoa). *Mar Biol* 147: 477–483.
- Pearse JS, Pearse VB (1978) Vision in cubomedusan jellyfishes. *Science* 199: 458.
- Garm A, Ekström P, Boudes M, Nilsson D-E (2006) Rhopalia are integrated parts of the central nervous system in box jellyfish. *Cell Tissue Res* 325: 333–343.
- Hou X-G, Stanley GD Jr, Zhao J, Ma X-Y (2005) Cambrian anemones with preserved soft tissue from the Chengjiang biota, China. *Lethaia* 38: 193–203.
- Van Iten H, De Moraes LJ, Simoes MG, Marques AC, Collins AG (2006) Reassessment of the phylogenetic position of conulariids (?Ediacaran-Triassic) within the subphylum medusozoa (Phylum Cnidaria). *J Syst Palaeontol* 4: 109–118.
- Hughes NC, Gunderson GO, Weedon MJ (2000) Late Cambrian conulariids from Wisconsin and Minnesota. *J Paleontol* 74: 828–838.
- Ross MI, Scotese CR (2000) *PaleoGIS/Arcview 3.5*. ArlingtonTexas: PALEO-MAP Project.